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The Orientation Selectivity Problem: An Approach from Theoretical Computer Science

方位選択性問題への理論計算機科学からのアプローチ

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1 Introduction

Neurobiologists [WH63] have found, in the primary visual cortex (area 17) of cat and monkey, some group of neurons that show “orientation selectivity”, or “orientation preference”. That is, each of such neurons reacts strongly to the presentation of light bars of certain orientation. Furthermore, there is some evidence that orientation selectivity is obtained in some animals through the training during the very early stage after the birth. Neuroscientists have proposed several models explaining this process of developing orientation selectivity [Mal73, Lin86, Mil92, MT92]. Furthermore, some of such models have been investigated mathematically [MM90, Tan90]. Yet, the mechanism that orientation selectivity emerges does not seem to be fully understood, and we may be able to get better understanding by investigating from different view points. In this paper, we will propose one approach that could be regarded as an approach from theoretical computer science. Here the emergence of orientation selectivity is formalized in terms of a simple mathematical model, on which we compare the behavior of several computational rules for the selectivity.

Researchers [Mil92, MT92] have pointed out that there are two key factors for the selectivity: (i) correlation between two types of inputs (i.e., ON- and OFF-center inputs), and (ii) some variation of Hebb’s learning rule for modifying synaptic strength. In fact, based on some hypothesis for (i) and (ii), mathematical models have been proposed to explain the selectivity, and the models have been tested mainly through computer simulation. In order to understand the mechanism and reasoning of the selectivity in more detail, we propose to consider the above two factors separately, and in this paper, we will focus on the second key factor. We simplify the emergence of orientation selectivity yet further, and reduce this into some simple mathematical game, “monopolists game”, on which we compare some learning rules (or, updating rules) and investigate whether orientation selectivity emerges following each of these rules.

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As a mechanism of changing synaptic strength, a “Hebb’s rule” may be the most acceptable one. Roughly speaking, Hebb’s rule can be stated as follows: the synaptic strength increase when both pre- and postsynaptic elements become active. But one can think of many variations of Hebb’s rule; some researchers [Mal73, Mil92, MT92] have used competitive variants of Hebb’s rule, which are essentially the same as the rule proposed by von der Malsburg [Mal73] (thus, we will call it von der Malsburg’s rule), for explaining a phenomenon like the orientation selectivity. Though von der Malsburg’s rule seems reasonable, it is still important to give mathematical justification to it and to search for some alternatives. The contribution of the paper is to explain, on our mathematical model, why von der Malsburg’s rule works, and investigate the behavior of some other possible rules.

Note that the orientation selectivity is developed from randomly given stimuli; thus, the process of developing the selectivity is not “learning”, because there is nothing to learn from random stimuli. That is, we discuss the mechanism of developing a somewhat organized structure by using less or not organized data. Previously, researchers [MM90, MM94] have mathematically investigated a feature of variants of Hebb’s rule such as von der Malsburg’s rule. But they discuss properties of Hebb’s rules as a *learning rule*, and thus, their results are yet not enough to understand fully the mechanism of developing the selectivity, i.e., developing a somewhat organized structure from random data. In this paper, we shed light on this point.

2 Von der Malsburg’s Computational Model

In his pioneer paper [Mal73], von der Malsburg gave the first reasonable explanation for developing orientation selectivity. Though his insight into the selectivity is still appreciated, the computational model that he used in his computer simulation is quite simple, and it has been taken over by more complicated and more biologically plausible models. Nevertheless, we use his model for our basic computational model. One reason is that it is much simpler. We also believe [SW97] that correlation between ON- and OFF-center inputs would provides us with the situation like von der Malsburg’s model. That is, the first of the two key factors for the selectivity gives some justification of using von der Malsburg’s computation model.

Here we first explain briefly the model considered by von der Malsburg.

Neural Network Structure

We consider two layer neural network, a input layer and a output layer. In particular, the output layer contains only one cell because we discuss here the orientation selectivity of one neuron. On the other hand, the input layer consists of 19 input cells that are (supposed to be) arranged in a hexagon like ones in Figure 1. We use i for indicating the i th input cell, and I for the set of all input cells. (Note that von der Malsburg studied the selectivity for a set of neurons; our neural network is a basic component of the one used in von der Malsburg’s experiment.)

Stimuli and Firing Rule

We use 9 stimuli with different orientations (Figure 2), which are given to the network randomly. Here • indicates an input cell that gets input 1, and o indicates an input cell that gets input 0.

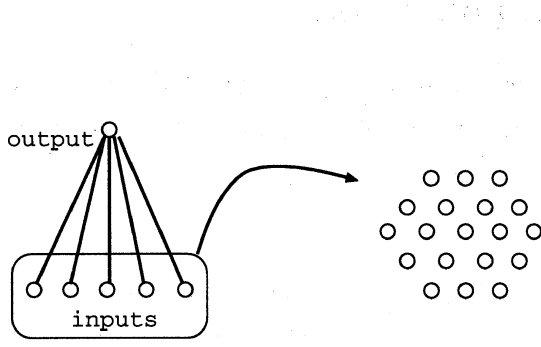


Figure 1: Neural network model.

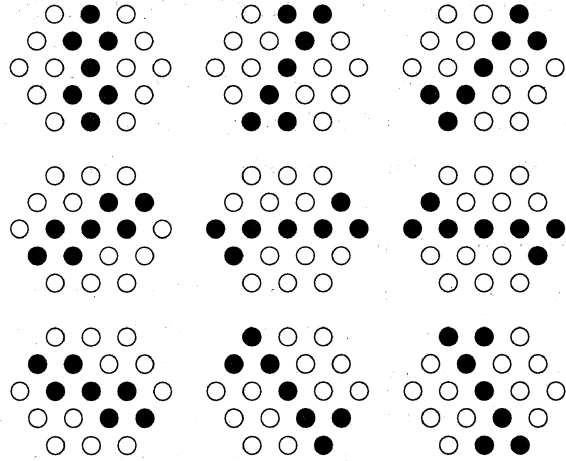


Figure 2: Nine stimuli.

We use A_i to denote input value (either 0 or 1) to the i th input cell. Then the output value V is computed in the following way:

$$V = Th_p \left(\sum_{i \in I} w_i A_i \right). \quad (1)$$

Where w_i is the current synaptic strength (which we simply call *weight*) between the output cell and the i th input cell. $Th_p(x)$ is a threshold function that gives $x - p$ if $x > p$ and 0 otherwise, where p is given as a parameter.

Learning Rule (Updating Rule)

Initially, each weight w_i is set to some random number between 0 to some constant. Then weights are updated each time according to the following variation of Hebb's rule, which we call *von der Malsburg's rule*:

$$\begin{aligned} w'_i &= w_i + c_{\text{inc}} A_i V, \text{ and} \\ w_i &= w'_i \times (W_0 / \sum_{k \in I} w'_k). \end{aligned} \quad (2)$$

Where c_{inc} (which is called a *growth rate*) and W_0 (*total weight bound*) are constants given as parameters. The first formula is the original Hebb's rule; on the other hand, the second one is introduced in order to keep the total weight within W_0 . (In fact, it is kept as W_0 .) Because of this second rule, some researchers do not consider it as Hebb's rule since it loses some feature of the original Hebb's rule.

With this setting, von der Malsburg demonstrated that the orientation selectivity occurs.

Criticism to von der Malsburg's Model

There have been several criticisms to the computation model of von der Malsburg. A crucial one is to the assumption of bar stimuli [Mil92]. This assumption may not be realistic; in fact, it has been reported that for some mammals, the orientation selectivity emerges before any visual stimulus is given. It is, however, by assuming a certain correlation between ON- and OFF-center inputs, we may be able to derive bar type stimuli (or, the effect of bar type stimuli) even from random noise on receptive fields [MM94, SW97].

3 Our Mathematical Model: Monopolist Game

In this paper, in order to give a formal proof to Malsburg's rule, and to investigate some other computation rules, we simplify von der Malsburg's computation model yet further. We propose the following simple probabilistic game for our preliminary investigation.

Monopolist Game

Rule: Initially n players are given the same amount of money. The game goes step by step, and at each step, one of the players win with the same probability. The winner gets some amount of money, while the other loses some.

Goal: The game terminates if all but one become bankrupt. If the survived player keeps enough money at that point, then he is called a *monopolist*.

The connection of this game to von der Malsburg's computation model is clear; player's wealth corresponds to total synaptic strength between the output cell and a set of input cells corresponding to one type of stimulus, and the emergence of monopolist means that the network develops the preference to one orientation. Thus, an updating rule of players' wealth corresponds to a rule of changing synaptic strength in the network. Here we consider updating rules described as below with some functions f_{dec} and f_{inc} . (In the following, let i_0 denote the player that wins at the current step.)

$$w_i = \begin{cases} w_i + f_{\text{inc}}(w_i) - f_{\text{dec}}(f_{\text{inc}}(w_i), w_i), & \text{if } i = i_0, \text{ and} \\ w_i - f_{\text{dec}}(f_{\text{inc}}(w_{i_0}), w_i), & \text{otherwise.} \end{cases} \quad (3)$$

Here f_{inc} and f_{dec} are functions that determine respectively the amount of increment and decrement at each step. One could think of more general cases such as these function values can depend on the status (i.e., wealth) of all players. But we will not go so further, because such general updating rules would lose biological justification. (We may use n' , the number of currently survived players, for computing f_{inc} or f_{dec} .)

From the relation to von der Malsburg's computation model, we require the following basic constrains: (i) both f_{inc} and f_{dec} are nondecreasing, and (ii) both $f_{\text{inc}}(0)$ and $f_{\text{dec}}(\delta, 0)$ are 0. Due to the second constraint, once the player loses all money, he stays forever in the 0 wealth state. (Note, on the other hand, that the player can still win with probability $1/n$.)

Here an updating rule is called a (variation of) *Hebb's rule* if it satisfies

$$f_{\text{inc}}(w_i) > f_{\text{dec}}(f_{\text{inc}}(w_i), w_i), \text{ and } f_{\text{dec}}(f_{\text{inc}}(w_{i_0}), w_i) > 0 \quad (4)$$

for any $w_i > 0$. That is, a winning player gains some amount of money, while the others loses some. All updating rules considered here essentially satisfy this condition. (There are some exceptional cases in some updating rule.) On the other hand, an updating rule is called *competitive* if f_{inc} and f_{dec} are defined so that the total amount of the wealth of all players is bounded.

Now let us define some updating rules. In this paper, we consider the following three updating rules:

- (1) von der Malsburg's rule, (2) local rule, and (3) semi local rule.

von der Malsburg's Rule

We begin with a rule corresponding to von der Malsburg's rule. It is defined as follows.

$$f_{\text{inc}}(w) = c_{\text{inc}}, \text{ and } f_{\text{dec}}(\delta, w) = \delta/n'. \quad (5)$$

(Here n' denotes the number of currently survived players. Note that from our basic requirement, we should define $f_{\text{inc}}(0) = 0$ as an exceptional case. In the following, we omit specifying this exceptional case.)

Note that with this rule, the total amount of wealth is kept constant. Thus, it is a competitive game.

We can consider a similar rule such that $f_{\text{inc}}(w)$ is not constant but proportional to w . (Similarly, $f_{\text{dec}}(w)$ is also proportional to w .) This rule might be closer to the original von der Malsburg's rule. But for discussing the probability of having a monopolist, the difference of two rules is not important; the difference disappears if we take log. Thus, we will discuss with our simpler rule.

Local Rule

In von der Malsburg's rule, updating function needs to know winner's profit; that is, updating values cannot be determined locally. Some researcher consider that such a computation rule is not biologically appropriate (though, for example, Tanaka [Tan90] gave a reasonable explanation to competitive rules from the limitation of growth factor). On the other hand, in order to be competitive, an updating rule cannot be local. To see the importance of competition, we consider here the following purely local updating rule.

$$f_{\text{inc}}(w) = c_{\text{inc}} \text{ and } f_{\text{dec}}(\delta, w) = c_{\text{dec}}. \quad (6)$$

Semi Local Rule

As a third updating rule, we consider somewhat mixture of the above two rules. It keeps a certain amount of locality, but it is still competitive. This rule is defined as follows.

$$f_{\text{inc}}(w) = \min(c_{\text{inc}}, W_0 - \sum_j w_j), \text{ and } f_{\text{dec}}(\delta, w) = c_{\text{dec}}. \quad (7)$$

That is, we want to keep the total wealth smaller than W_0 . Thus, a winner can gain c_{inc} (in net, $c_{\text{inc}} - c_{\text{dec}}$) if there is some room to grow. In this case, each player (more precisely, a winner) only needs to know the total amount of wealth, or the amount of space left.

4 Analysis of Updating Rules

Here we analyze our three updating rules, and investigate the probability P_* that a monopolist emerges. For von der Malsburg's rule, we give the proof that $P_* = 1$. On the other hand, for the local rule, we give some mathematical explanation that P_* is fairly small, and justify it by experimental results. For the semi local rule, while we have not been able to give good mathematical explanation, we show that P_* is large through some experiments.

In the following, we assume that $c_{\text{dec}} = 1$.

von der Malsburg's Rule

Random walk is our basic mathematical tool for the analysis. Here we consider one-dimensional random walk of a particle in a given interval $[u, v]$ (Figure 3). (We assume that u and v are integers, and that the particle stays on only integer position.)

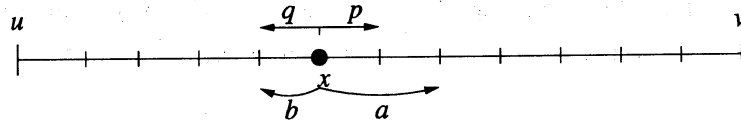


Figure 3: One-dimensional random walk.

Initially, the particle is on given initial position x . In one step, it moves a to the right with probability p , and b to the left with probability $q = 1 - p$. The end of the interval is either an *absorbing wall* or a *reflecting wall*. An absorbing wall keeps the particle forever, while a reflecting wall bounce back the particle. That is, once the particle reaches to an absorbing wall, it stay there forever. On the other hand, the particle that reaches to a reflecting wall is moved b to the left (or, a to the right) in the next step.

We make use of the following fact[Fel68].

Proposition 4.1. Consider a one-dimensional random walk in an interval with absorbing walls on both ends. Then for any choice of a , b , p , and x , with probability 1, the particle is absorbed one of the ends in finite steps.

Theorem 4.2. Under von der Malsburg's rule, a monopolist emerges (in finite steps) with probability 1.

Proof. By induction on the number of players, we show that all but one players go into bankruptcy with probability one. Notice that the sum of all players' wealth is kept the same; thus, the survived one, who takes all the wealth, can be regarded as a monopolist.

We consider for the base case, the game with two players 1 and 2. We focus on the player 1's wealth, which follows the following random walk.

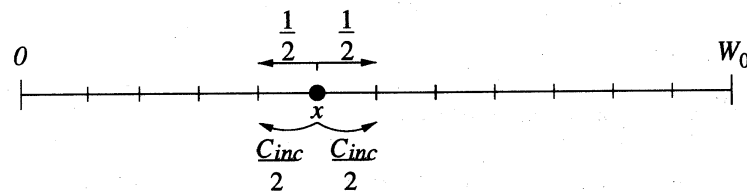


Figure 4: Player 1's wealth

Here $W_0 = w_1 + w_2$ is the total amount of wealth. Thus, if the particle reaches to W_0 , then the player 2 become a bankrupt, while if the particle reaches to 0, then the player 1 become a bankrupt. Now it follows from Proposition 4.1 that the particle is absorbed to one of the walls with probability 1; thus, either the player 1 or the player 2 becomes a monopolist with probability 1.

The induction step is proved similarly. Here again we consider the wealth of one player i , and the right end is W_0 . Thus, if the particle reaches to the right end, then the player i becomes a monopolist. On the other hand, if it reaches to 0, then the player i becomes a bankrupt and get removed from the game. (Precisely speaking, even a bankrupt wins with probability $1/n$. But since a bankrupt get nothing, everything remains the same; thus, we can ignore such a case.) \square

Local Rule

First we estimate, for a given W , the probability $P_{x,W}$ that one player, say player 1, obtains W at some point in the game. For this we use the following fact[Fel68].

Proposition 4.3. Consider one-dimensional random walk following the figure below, and assume that the particle is initially on position x . Then the probability $P_{x,W}$ that the particle reaches W is $\frac{x}{W+n-2} \leq P_{x,W} \leq \frac{x}{W}$.

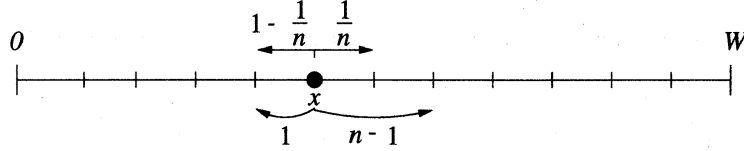


Figure 5: Random walk representing one player's wealth.

We also want to estimate the probability \bar{P}_x that player 1 becomes a bankrupt. For approximating \bar{P}_x , we use here the probability $\bar{P}_{x,W}$ that player 1 becomes bankrupt in the same random walk as Proposition 4.3. That is, we approximate \bar{P}_x as $\lim_{W \rightarrow \infty} \bar{P}_{x,W}$.

Proposition 4.4. [Fel68] As W goes to ∞ , $\bar{P}_{x,W}$ converges to 1 if $c_{\text{inc}} \leq n$; otherwise it converges to some number $\leq (1 - 1/n)^x$.

Now let P_* be the probability that at some point in the game, all but one become bankrupt, and the survived player has wealth W , for sufficiently large W ; that is, P_* is the probability that a monopolist emerges. We want to bound this probability from the above.

Clearly, if some player becomes a monopolist, then he must at least reach to W , and its probability is at most x/W by Proposition 4.3. Thus, the probability that someone becomes a monopolist is at most nx/W .

Here for another upper bound, we use the probability P'_* that exactly one player has ever reached to W in the game. If W is sufficiently large, it is quite unlikely that players who have reached to W become bankrupts. Hence if more than one player reaches to W at some point in the game, then we may assume that a monopolist does not occurs in this game. Thus, we may be able to consider that $P_* < P'_*$. Then we prove the following bound for P'_* .

Theorem 4.5. For sufficiently large W , we have $P'_* \leq \frac{1}{2} + \varepsilon$, where ε can be made arbitrarily small by using appropriate x for each n .

Proof. Consider P'_* with sufficiently large W . Note first that

$$\begin{aligned} \Pr\{\text{All players become bankrupts}\} &= (\bar{P}_{x,W})^n, \\ \Pr\{\text{just one player's wealth reaches to } W\} &= n(1 - \bar{P}_{x,W})(\bar{P}_{x,W})^{n-1}, \text{ and} \\ \Pr\{\text{more than one player's wealth reach to } W\} &= 1 - (\bar{P}_{x,W})^n - n(1 - \bar{P}_{x,W})(\bar{P}_{x,W})^{n-1}. \end{aligned}$$

Then by definition of P'_* , we have

$$\begin{aligned} P'_* &< 1 - (\bar{P}_{x,W})^n, \text{ and} \\ P'_* &< 1 - \Pr\{\text{more than one player's wealth reach to } W\} \\ &= (\bar{P}_{x,W})^n + n(1 - \bar{P}_{x,W})(\bar{P}_{x,W})^{n-1}. \end{aligned}$$

Hence,

$$P'_* < \frac{1}{2} + \frac{n}{2}(1 - \bar{P}_{x,W})(\bar{P}_{x,W})^{n-1}.$$

Now, since we are considering the case that W is large enough, we can use \bar{P}_x instead of $\bar{P}_{x,W}$. By Proposition 4.4, we get

$$P'_* < \begin{cases} \frac{1}{2} & c_{\text{inc}} \leq n, \\ \frac{1}{2} + \frac{n}{2}(\frac{1}{e})^{(x-1/n)} & \text{o.w..} \end{cases}$$

By taking $x > \ln n + c$, we can make $\frac{n}{2}(\frac{1}{e})^{(x-1/n)}$ small enough. \square

Semi Local Rule

Again we begin with reviewing our experiment. The following Table 3 shows the results of 1,000 games for $n = 10$ and for each c_{inc} value. For the initial value, we use 10. For W_0 , the bound of total wealth, we use $n \times 10$. The structure of the table is the same as Table 1: column N shows the number of games that eventually had one survivor. Based on the amount of wealth that survivor poses at the end, these games are classified into four groups, and the next four columns (N_1, N_2, N_3, N_4) indicates the number of games in each group. Since the total wealth bound W_0 is 100, we may be able to consider that N_4 is the number of games that a monopolist emerges.

Table 3: Semi local rule.

# of players : 10					
C_{inc}	N	N_1 1 ~ 25	N_2 26 ~ 50	N_3 51 ~ 75	N_4 76 ~ 100
8	957	577	322	56	2
10	996	192	381	295	128
12	998	63	209	341	385
14	1000	25	121	329	525
16	1000	16	67	275	642
18	1000	8	59	231	702
20	1000	6	44	193	757

As we see, the probability P_* that a monopolist emerges is fairly large if c_{inc} is large enough. Although we have not been able to prove this property, we can give some (both experimental and analytical) results supporting it.

We compare the random walk representing the total wealth, *the random walk for the total*, with the random walk representing the wealth of currently the poorest player, *the random walk for the poorest*. For the case with n' players left, these random walks are expressed as follows.

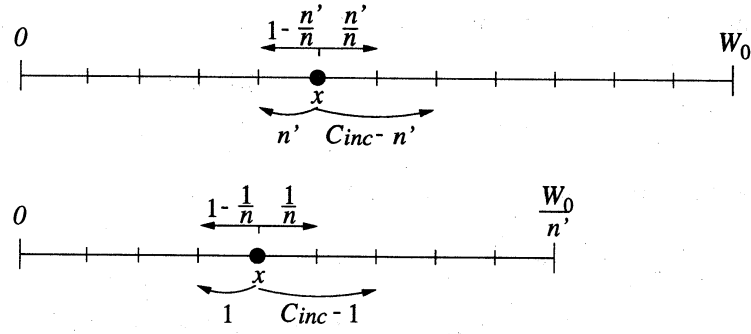


Figure 6: Random walk for the total (above) and for the poorest (below)

Since the total wealth is at most W_0 , the poorest player cannot have more than W_0/n' . Also as soon as the poorest player obtains W_0/n' , he cannot be the poorest, and he is replaced by some currently poorest player, whose wealth is again less than W_0/n' . In any case, if we only consider the wealth of the poorest player, we can assume that the rightmost end is a reflecting wall. For the random walk for the total wealth, the rightmost end is a reflecting wall, too, because of the upper bound W_0 and the updating rule. Thus, in both random walks, the rightmost walls are reflecting walls; hence, the particles are eventually absorbed in the leftmost walls. Here we show the difference between the number of steps until the particles are absorbed.

Here we prove the following result.

Theorem 4.6. For any n' , $2 \leq n' \leq n$, consider the random walks corresponding to the monopolist game with n' players left, and let t_1 and t_{all} denote the average number of steps that the particle is absorbed in the random walk for the poorest and in the random walk for the total respectively. If $c_{inc} > 2n$, then we have $t_1 - t_{all} > W/2$.

Proof. We consider only the case n' is 2 because in this case t_{all} is the smallest while t_1 is the largest. In this case, on the random walk for the poorest, by multiplying by 2 to starting position, upper bound and amounts of movement, and normalizing amounts of movement, then random walks for the total and for the poorest are revised as below, where $c = c_{inc} - 2c_{dec}$.

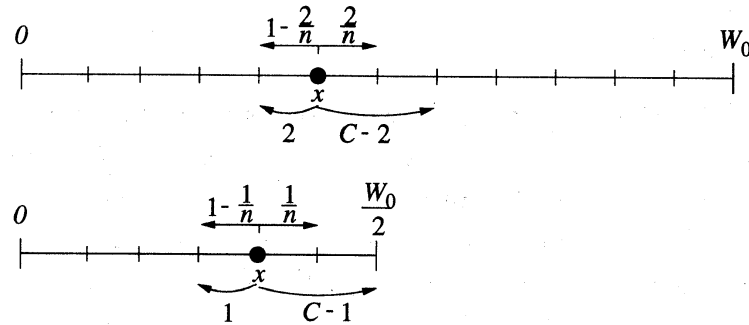


Figure 7: Random walk for the total (above) and for the poorest (below) in case of $n' = 2$

Let x_k be the random variable that denoting the number of steps starting off at k and arriving at $k - 1$ for the first time.

On the random walk for the total, we can evaluate x_k by

$$x_k = \begin{cases} 1 & \text{with probability } 1 - 2/n, \\ 1 + x_{k+c} + x_{k+c-1} + \dots + x_k & \text{o.w.} \end{cases}$$

Define e_k to be the expectation of x_k . Then we have

$$\begin{aligned} \left(1 - \frac{2}{n}\right)e_k &= 1 + \frac{2}{n}(e_{k+c} + \dots + e_{k+1}), \\ e_k &\approx 1 + \frac{2}{n}(e_{k+c} + \dots + e_{k+1}). \quad (\text{since } \frac{n-2}{n} \approx 1 \text{ for large } n) \end{aligned}$$

On the other hand, On the random walk for the poorest,

$$e'_k \approx 1 + \frac{1}{n}(e'_{k+2c} + \dots + e'_{k+1}).$$

Since $t_{\text{all}} = \sum e_k$ and $t_1 = \sum e'_k$ ($1 \leq k \leq W$), we have,

$$\begin{aligned} t_{\text{all}} - t_1 &= (e_W - e'_W) + \dots + (e_1 - e'_1) \\ &= 1 + \frac{2}{n}(e_{W+c} + \dots + e_{W+1}) - 1 + \frac{1}{n}(e'_{W+2c} + \dots + e'_{W+1}) \\ &\quad + \dots + 1 + \frac{2}{n}(e_{c+1} + \dots + e_2) - 1 + \frac{1}{n}(e'_{2c+1} + \dots + e'_1) \\ &\geq \frac{1}{n}(e_{W+c} + \dots + e_{W+1}) - \frac{1}{n}(e'_{W+2c} + \dots + e'_{W+c+1}) \\ &\quad + \dots + \frac{1}{n}(e_{c+1} + \dots + e_2) - \frac{1}{n}(e'_{2c+1} + \dots + e'_{c+2}) \quad (\text{since } e_k > e'_k) \\ &= \frac{1}{n}(e_{W+c} + \dots + e_{W+1}) - \frac{1}{2}(e_{W+c} - 1) \\ &\quad + \dots + \frac{1}{n}(e_{c+1} + \dots + e_2) - \frac{1}{2}(e_{W+1} - 1). \\ &\quad (\text{since } e_k = 1 + \frac{2}{n}(e_{k+c} + \dots + e_{k+1}), \frac{1}{n}(e_{k+c} + \dots + e_{k+1}) = \frac{1}{2}(e_k - 1)) \end{aligned}$$

For $c \geq n/2$, since $e_k < e_{k-i}$, we have

$$\frac{1}{n}(e_{W+c} + \dots + e_{W+1}) > \frac{1}{2}e_{W+c}.$$

Therefore $t_{\text{all}} - t_1 > W/2$. \square

Therefore, from the situation that n' players left, we can expect that one of them disappears before all players go into bankruptcy. It is easy to see that the most competitive case is the case with two players left. Even in such a case, our experiment (Table 4 below) shows that the poorest player's wealth decreases much faster than the total amount of wealth if c_{inc} is sufficiently large. (The table shows the number of steps that the particle is absorbed into the leftmost end in the random walk for the poorest (left) and in the random walk for the total (right). The numbers are average of 100 random walks.)

Table 4: Average steps to bankruptcy.

# of players : 10					
C_{inc}	poorest	total	C_{inc}	poorest	total
1	62.74	71.11	11	479.64	7477.60
3	82.14	96.14	13	707.1	25785.76
5	116.03	146.94	15	885.99	65456.82
7	176.67	302.76	17	1086.76	122284.08
9	293.8	1226.33	19	1317.42	206277.20

Conclusion

In order to understand the reason for orientation selectivity, we first proposed to simplify its mechanism by separating it into the following two parts: (i) the part that extracts bar stimuli from random noise, and (ii) the part that induces the selectivity when given bar stimuli of random orientation. Then, in this paper, we focus on the second part, and introduce “monopolist game” as a simplified model for studying a learning rule in this second part.

On this monopolist game, we investigate, for some learning rules, whether it leads to orientation selectivity, or more precisely, a configuration corresponding to the selectivity. As a result, we prove that von der Malsburg’s rule (i.e., the rule corresponding to the learning rule used in von der Malsburg’s model) indeed induces orientation selectivity with probability 1. We also consider two local rules for the other possible learning rules. We prove that the selectivity does not emerge (with high probability) with a pure local rule. On the other hand, we show by computer simulation that the selectivity occurs with fairly high probability with a variation of local rule with some global constraint. We also prove some evidence supporting this computer simulation. On the other hand, it is difficult to provide stable configurations with local rules. Therefore, we can conclude that von der Malsburg’s rule, which provides both selectivity and stable configurations, is most appropriate for orientation selectivity mechanism.

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